

THE IMPACT OF SALAMANDER PREDATION ON COLLEMBOLA ABUNDANCE

THOMAS P. ROONEY, CHRISTOPHER ANTOLIK, AND MATTHEW D. MORAN

(TPR) Department of Botany, University of Wisconsin, 430 Lincoln Drive, Madison, WI 53706, U.S.A. (e-mail: tprooney@students.wisc.edu); (CA) Department of Biology, University of Delaware, Newark, DE 19716, U.S.A.; (MDM) Department of Biology, 1600 Washington Ave., Hendrix College, Conway, AR 72032, U.S.A. (e-mail: moran@mercury.hendrix.edu)

Abstract.—We examined the role of the red-backed salamander, *Plethodon cinereus*, in controlling springtail (Collembola) abundance in a temperate deciduous forest. Salamander abundance was manipulated in paired, replicated field enclosures during fall 1993 and spring 1994, such that each cage either had four or zero salamanders m^{-2} . After four weeks we sampled arthropod abundance with pitfall traps. The abundance of arthropods was compared using two-way MANOVA (treatments = salamanders and season), followed by univariate tests for each taxon. The effects of salamanders on arthropods was not significant (Wilks' $\lambda = 0.76$, $P = 0.6$), but Collembola were significantly more abundant in the presence of salamanders. Season had a significant effect on arthropod abundance (Wilks' $\lambda = 0.13$, $P < 0.0001$); beetles, crickets, millipedes, and mites were more abundant in the fall, and Collembola were more abundant in the spring. Stomach analysis of salamanders showed that ants were their main prey item, and Collembola were not among the prey taken. We hypothesize that salamanders indirectly enhanced Collembola abundance by preying upon their invertebrate predators.

Key Words: detrital food web, food web manipulation, predator-prey interactions, deciduous forest, field experiment, predation

Arthropods such as Collembola (springtails) are often abundant in forest litter, occasionally reaching densities of thousands to tens of thousands m^{-2} (Christiansen 1964, Peterson and Luxton 1982, Blair et al. 1994). Their activities affect rates of litter decomposition and nutrient cycling (Crossley 1977, Schaefer 1990). However, little is known about factors that limit or regulate the abundance of these arthropods (Schaefer 1990). Some empirical studies indicate that "bottom-up" forces such as soil moisture content determine Collembola abundance (Joosse and Testerink 1977, Testerink 1981, Vegter 1987) while others have

demonstrated that "top-down" forces such as arthropod predators limit their abundance (Clarke and Grant 1968, Ernsting and Joosse 1974, Ernsting 1977).

One guild of predators with the potential to influence arthropods in forest floor ecosystems is terrestrial salamanders. Burton and Likens' (1975) calculations estimate that energy flow through salamander populations is equal to one complete turnover of the soil fauna each year (Hairston 1987). Salamanders are generalist predators that feed on a variety of detritivorous, herbivorous, and predatory arthropods, including Collembola (Burton 1976, Mitchell and

Woolcott 1985, Pauley 1995, Maglia 1996, Wyman 1998). Because salamanders feed on both Collembola and their arthropod predators, salamanders may exhibit both direct and indirect effects on Collembola (Spiller and Schoener 1988, Moran et al. 1996).

Here we report a field experiment that tested the hypothesis that salamanders limit collembolan abundance through a direct predator-prey interaction. We tested this hypothesis by manipulating densities of the red-backed salamander, *Plethodon cinereus*, in replicated field cages in a forest ecosystem, and measuring the numerical response of the arthropod community to salamanders 4 weeks later. We combined this field manipulation with an examination of salamander stomach contents to correlate salamander feeding with its possible effects on Collembola.

MATERIALS AND METHODS

We performed experiments at an old growth, mixed hardwood deciduous woodland in the Piedmont province of northern Delaware (west of Pike Creek, New Castle County). The canopy species in descending order of abundance were *Fagus grandifolia* Ehrh., *Liriodendron tulipifera*, *Quercus rubra* L., and *Carya glabra* (Miller) Sweet. Sub-canopy trees included *Acer rubrum* L., *A. saccharum* Marsh., *Cornus florida* L., and *Fagus grandifolia* Ehrh.

Plethodon cinereus was the only salamander encountered at our site. We established a 10- × -5 m grid with 1-m² quadrats to determine population density of salamanders in our field site, so that we could later establish treatment densities within the range of naturally occurring densities. During a wet period, when salamanders were active at the surface, we searched the entire grid. Mean density of salamanders was 0.56 individuals m⁻², which is comparable with results from other studies (Hairston 1987). Local densities reached 5 individuals m⁻² in favorable sites, such as under coarse woody debris.

To manipulate local salamander densities for our experiment, we used 14 1-m³ PVC frame enclosures completely covered with a 1 mm nylon mesh (Bioquip Products, Gardena, CA) so that organisms larger than Collembola could not enter or exit cages. We sunk these enclosures 20 cm into the ground to prevent salamander movement under them. We arranged enclosures in a 7- × -2 array spaced at approximately 1.5-m intervals. Before manipulation of density within enclosures, removed salamanders that were present.

Four adult salamanders (5–8 cm) of unknown sex were added to treatment enclosures, whereas reference enclosures contained no salamanders. Treatment and reference enclosures were paired, and treatments alternated systematically along the array (Hurlbert 1984). We placed a single 8-cm wide, 12-cm deep plastic cup (approximately 475 ml) in the center of each enclosure before initiating the experiment. Four weeks after salamander introduction, covers were removed from the traps and approximately 50 ml of 95% ethanol was added to each trap. Traps were left open for 48 h, then removed and taken back to the lab. We counted Collembola > 0.5 mm and other arthropods under a dissecting microscope. Flies (Diptera), centipedes (Chilopoda), and earwigs (Dermaptera) numerically comprised < 0.5% of all taxa captured and were not included in the analysis. Our experiment was conducted in the fall 1993 and again in spring 1994. Taxon abundance was analyzed using a two-way MANOVA (factors = salamanders and season). Although Collembola are of immediate interest, MANOVA provides both a global test of treatment effects on all arthropods, as well as a protected F procedure for each taxon to reduce the probability of a type I error (Manly 1994). Two-way MANOVA allows us to account for variation due temporal changes in Collembola abundance while analyzing the variable of greater interest: the impacts of salamanders on Collembola. Because collembola abundance

Table 1. Mean number (± 1 SE) of arthropods captured in pitfall traps in treatment and reference enclosures in fall 1993 and spring 1994, New Castle Co., Delaware. Within taxa, means followed by different letter superscripts are different at the $\alpha = 0.05$ based on Fisher's L.S.D. test.

Taxon	Fall Enclosure		Spring Enclosure	
	Treatment	Reference	Treatment	Reference
Collembola	50.5 (8.8) ^b	23.9 (2.6) ^a	167.7 (28.9) ^c	154.1 (41.1) ^c
Acari	31.0 (10.1) ^b	23.9 (2.6) ^b	0.1 (0.1) ^a	— ^a
Araneae	1.0 (0.5) ^a	0.3 (0.2) ^b	— ^a	— ^a
Coleoptera	2.4 (0.5) ^b	2.0 (0.6) ^b	0.5 (0.2) ^a	— ^a
Orthoptera	0.9 (0.5) ^b	0.7 (0.5) ^b	— ^a	— ^a
Spirobolida	1.4 (0.7) ^b	0.7 (0.4) ^b	— ^a	— ^a
Hymenoptera	0.4 (0.4) ^a	0.3 (0.1) ^a	0.5 (0.4) ^a	1.9 (1.3) ^a

was not normally distributed, it was log transformed prior to analysis. We considered patterns significant if $P \leq 0.05$.

After the spring field experiment was completed, we collected 12 adult salamanders from the study site for stomach analysis. These salamanders were the same size as those used in the experiment and were presumably feeding on the same prey base. Stomachs were removed and preserved in 95% ethanol. We removed arthropod remains from stomachs and sorted them according to taxonomic order.

RESULTS

Collembola was the most abundant arthropod taxon captured in pitfall traps, accounting for 75.1% of all individuals. Treatment enclosures did not contain more arthropods than reference enclosures (Wilks' $\lambda = 0.76$, $F_{7,18} = 0.79$, $P = 0.60$). However, there were significantly more Collembola in salamander enclosures than reference enclosures ($F_{1,24} = 4.30$, $P = 0.049$, Table 1). Abundance of other arthropod taxa was not significantly affected by the presence of salamanders. In contrast, season had a significant effect on the abundance of arthropods captured (Wilks' $\lambda = 0.13$, $F_{7,18} = 17.63$, $P < 0.0001$). There were significantly more beetles (Coleoptera; $F_{1,24} = 21.23$, $P = 0.0001$), crickets (Orthoptera; $F_{1,24} = 5.67$, $P = 0.03$), millipedes (Spirobolida; $F_{1,24} = 7.11$, $P = 0.01$), and oribatid mites (Acari; $F_{1,24} = 13.56$, $P = 0.001$) captured in the

fall, and more Collembola ($F_{1,24} = 60.73$, $P < 0.0001$) captured in the spring. Spiders (Araneae) and ants (Hymenoptera: Formicidae) did not significantly differ between seasons (Table 1). The interaction between salamanders and season was not significant (Wilks' $\lambda = 0.82$, $F_{7,18} = 0.57$, $P = 0.77$).

Eighty-nine prey items were found in 12 salamander stomachs. Ants were the majority of arthropods eaten by salamanders, numerically accounting for 56% of all individuals found. Mites (Acari) accounted for 28% of the individuals, and Pseudoscorpiones, Coleoptera, Chalcidoidea, and Hemiptera made up the remaining 13%.

DISCUSSION

We initially hypothesized that salamanders would reduce Collembola abundance by direct predation. However, our field experiment showed the opposite phenomenon: Collembola abundance increased in the presence of salamanders. Salamander stomachs did not contain any Collembola, even though this taxon was the most abundant forest-floor arthropod. Since the major prey for salamanders at our study site were ants, we hypothesize that Collembola abundance was enhanced by a reduction of its invertebrate predators. Indirect effects such as this have been shown to be common in many vertebrate-arthropod food webs (Spiller and Schoener 1988, Altegrim 1989) and may be operating in this system. However, we did not detect a reduction in ants

or other carnivorous arthropods within our enclosures. Without further data, the mechanisms by which salamanders influence collembolan abundance will remain unresolved.

Our results suggest collembolan abundance may be enhanced by salamander predation on collembolan predators, particularly ants. Many ant species are omnivorous, although some groups of ants (tribe Dacetini) specialize on *Collembola* (E. O. Wilson, personal communication). Ants are also preyed upon by salamanders (Mitchell and Wollcott 1985, Maglia 1996, Wyman 1998), and made up the largest proportion of salamander prey items in this study. Oddly, we captured very few ants in the pitfall traps (Table 1). William J. Dress (personal communication) observed that ants were proficient at avoiding capture by pitcher plants, which leads us to suspect ants may have avoided our pitfall traps as well. Alternatively, the ethanol in the traps may have repelled ants. It is quite possible that ants may have been under-represented in our pitfall traps.

There was a significant seasonal effect on arthropod abundance. In seasonal temperate environments like our study site, insects with a semelparous, univoltine life cycle are killed each fall by cold, and eggs or other stages overwinter. It is likely that many of the taxa that were less abundant in the spring because the experiment was conducted prior to or shortly after egg hatch. *Collembola* are active year round (Christiansen 1964) and population sizes are known to vary seasonally in response to moisture availability (Vegter 1987). Spring in northern Delaware is characterized by cool temperatures and abundant precipitation, which may favor collembolan populations in spring compared to the area's warmer and drier fall. Alternatively, collembolan populations may be more active in the spring when conditions are more favorable than other seasons, which could account for the difference in abundance between the fall and spring.

Short-term studies such as this one provide insights into how species might be connected in food webs. However, because the strength of any pairwise interaction often varies in space and time, the enhancement of collembolan abundance by salamanders should not be generalized to other sites, nor do we expect enhancement to occur every year at our study site (Magnuson 1990). Instead, our results indicate that salamanders can exhibit positive, indirect effects on *Collembola* that could outweigh the direct effects of predation. Further long-term studies into detrital food web structures and dynamics are needed to understand the numeric relationships between salamanders, *Collembola*, and other forest floor arthropods.

ACKNOWLEDGMENTS

We thank an anonymous reviewer for helpful suggestions on an early draft of this paper, and the Downs Conservancy for allowing us to work on its property.

LITERATURE CITED

- Altegrim, O. 1989. Exclusion of birds from bilberry stands: impact on insect larval density and damage to bilberry. *Oecologia* 79: 136-139.
- Blair, J. M., R. W. Parmelee, and R. L. Wyman. 1994. A comparison of the forest floor invertebrate communities of four forest types in northeastern U.S. *Pedobiologia* 38: 146-160.
- Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *Journal of Herpetology* 10: 187-204.
- Burton, T. M. and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* 56: 1068-1080.
- Christiansen, K. 1964. Bionomics of *Collembola*. *Annual Review of Entomology* 9: 147-178.
- Clarke, R. D. and P. R. Grant. 1968. An experimental study of the role of spiders as predators in a forest floor litter community. Part 1. *Ecology* 49: 1152-1154.
- Crossley, D. A., Jr. 1977. The roles of terrestrial saprophagous arthropods in forest soils: Current status and concepts, p. 49-56. *In* Mattson, W. J., ed., *The Role of Arthropods in Forest Ecosystems*. Springer-Verlag, New York, New York, USA, 104 pp.

- Ernsting, G. 1977. Aspects of predation and the co-existence of springtail prey species. *Ecological Bulletin* 25: 478-480.
- Ernsting, G. and E. N. G. Jooose. 1974. Predation on two species of surface dwelling Collembola: A study with radio-isotope prey. *Pedobiologia* 14: 222-231.
- Hairston Sr., N. G. 1987. *Community Ecology and Salamander Guilds*. Cambridge University Press, New York, New York, USA, 230 pp.
- Hurlbert, S. H. 1984. Pseudoreplication and design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Jooose, E. N. G. and G. S. Testerink. 1977. The role of food in the population dynamics of *Orchesella cincta* (Linne) (Collembola). *Oecologia* 29: 189-204.
- Maglia, A. M. 1996. Ontogeny and feeding ecology of the red-backed salamander, *Plethodon cinereus*. *Copeia* 1996: 576-586.
- Magnuson, J. J. 1990. Long-term ecological research and the invisible present. *BioScience* 40: 495-501.
- Manly, B. F. J. 1994. *Multivariate statistical methods: a primer*. 2nd ed. Chapman and Hall, New York, USA, 215 pp.
- Mitchell, J. C. and W. S. Woolcott. 1985. Observations of the microdistribution, diet, and predator-prey size relationships in the salamander *Plethodon cinereus* from the Virginia piedmont (USA). *Virginia Journal of Science* 36: 281-288.
- Moran, M. D., T. P. Rooney, and L. E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. *Ecology* 77: 2219-2227.
- Pauley, T. K. 1995. Terrestrial salamanders, p. 42-52. *In* Reardon, R. C., ed., *Effects of Diflufenzuron on Non-target Organisms in Broadleaf Forested Watersheds in the Northeast*. U.S.D.A. Forest Service Technical Publication F-UM-NC-05-1995. 174 pp.
- Petersen, H. and M. Luxton. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39: 288-388.
- Schaefer, M. 1990. The soil fauna of a beech forest on limestone: Trophic structure and energy budget. *Oecologia* 82: 128-136.
- Spiller, D. A. and T. W. Schoener. 1988. An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs* 58: 57-77.
- Testerink, G. S. 1981. Starvation in a field population of litter inhabiting Collembola: Methods for determining food resources in small arthropods. *Pedobiologia* 21: 427-432.
- Vegter, J. J. 1987. Phenology and seasonal resource partitioning in forest floor Collembola. *Oikos* 48: 175-185.
- Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: Effects on invertebrates, decomposition, and the carbon cycle. *Biodiversity and Conservation* 7: 641-650.